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The development of the sexual organs and sporogonium of Marchantia polymorpha*

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(WITH PLATES 21–25)

For some time past the writer has been preparing sets of slides for the use of students in a course in embryology. The aim has been to get together series as complete as possible to illustrate the important steps in the development of at least one representative of each of the great groups of green plants. The slides when finished are numbered, and each valuable section on the slide is marked and numbered. The stages represented are then carefully arranged in sequence and outlines prepared in which they are indicated in their proper order with the numbers of the slides and sections in which they appear. In this way the student, having had all the sections found, marked, and arranged for him, and having to waste no time in searching for the desired stages, can study the maximum amount of material in the minimum of time.

It should be emphasized that such slides are not intended to take the place of but to supplement those which the student makes for himself in order to get training in the methods used in the preparation of such material. It will be readily understood that to get together series of this kind requires much time and patience, but the writer feels that the outlay is fully justified by the results obtained. The student who goes over a set of preparations such as is illustrated in the present paper, making drawings of all the stages, and finally writing up for himself an account of the development of the plant based on his own studies and drawings has at

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the end a feeling of satisfaction in having acquired a fairly comprehensive knowledge of the embryology of that species and of the group to which it belongs. Moreover, the preparation of such sets may prove to be of almost as much value to the teacher as to the student.

As the representative of the Marchantiaceae the writer naturally selected *Marchantia polymorpha*, it being the most accessible as well as the most easily studied member of the group. An examination of what has been written concerning this species brought out a rather surprising state of affairs. *Marchantia polymorpha* has long been a favorite object for class study. It has been described and illustrated in practically every textbook treating of the liverworts, and has been made the subject of numerous investigations, so that it would seem as if nothing remained to be done with it. Yet nowhere has there ever been published an even approximately complete account of the development of the antheridia, archegonia, and sporogonia of this species, nor anything approaching a complete series of figures illustrating these phenomena.

Inasmuch as this plant is so commonly used in class work it has seemed to the writer to be desirable that a fairly complete series of illustrations should be available for the use of students. The accompanying figures with the brief account of the development of the sexual organs and sporogonium are therefore presented in the hope that they may be found useful.

Marchantia grows commonly on damp soil in ravines or along wood-roads, but reaches its best development on damp, burnt soil. The writer once visited a burnt-out swamp several acres in extent in which the ground was nearly completely covered with luxuriant thalli to a depth in some places of several inches. The gametophores begin to appear early in May, and the sporogonia mature in July.

ANTHERIDIUM

The antheridia of *Marchantia* are sunk in cavities in the upper surface of the antheridiophore. They develop in acropetal succession, the youngest being near the margin and the oldest near the center of the disk. They do not originate from all portions of the margin equally but the younger ones are produced in certain

definite meristematic regions which lie between the lobes. Goebel regards the antheridiophore as representing an entire branching system, which divides repeatedly, the apices being near the margin and constituting the meristematic regions mentioned. While young antheridia may be found on quite large receptacles, it is best to collect the smaller ones in which the stalk is still very short or even has not begun to elongate. The material from which the present study was made was collected May 26, 1900, and fixed in Flemming's solution. The sections are 8–10 μ thick and stained in Delafield's hematoxylin. This stain is well adapted to work of this kind since it brings out the cell-walls and nuclei very clearly.

The youngest antheridium that I have been able to recognize definitely as such is shown in *figure 1*. It is a conical cell several cells removed from the margin, and has evidently been cut off by a transverse wall from the cell beneath it. A study of the section shows that the neighboring cells also have been derived in the same manner from the cells beneath. An examination of many preparations of young stages has convinced me that the antheridial rudiment of *Marchantia* at no time projects above its fellows later to become buried, but is one of the superficial, dorsal, submarginal cells of the receptacle, having the same origin and being cut off at practically the same time as the cells adjacent to it, but soon becoming separated from them, assuming a conical form, and becoming richer in protoplasmic contents. The one shown in *figure 1* has already been slightly surpassed by the elongating adjacent cells.

In the stage shown in *figures 2* and *3*, the rudiment has been divided by a transverse wall into two cells, the proximal being the mother-cell of the stalk, while the distal is the mother-cell of the antheridium proper. Occasionally the receptacle is so convex above that the young antheridia are nearly horizontal so that transections of the gametophore give longisections of the young organ (*figs. 4–6*).

The young antheridium now enlarges (*figs. 4, 5*) and soon becomes sunk in a cavity owing to the division and upward growth of the surrounding cells (*fig. 6*). The divisions in the lower cell to form the stalk follow no regular order but may be either longi-

tudinal or transverse or both, as may be seen by inspection of *figures 9–24*. In the distal or antheridial cell, however, the divisions are regular. It soon segments transversely into either two (*figs. 7–12*), or three (*figs. 13–20*), or perhaps rarely four cells (*cf. figs. 21, 23*). I have not seen more than two transverse walls in any antheridium at this age, a greater number of walls, so far as my observation goes, always appearing in organs which have progressed considerably in their development, so that they were probably formed subsequently to vertical division (*cf. figs. 24, 25*). Each cell of the antheridium now soon divides by a vertical wall into two. This division usually appears first in the proximal cells (*figs. 10, 14–18*), but occasionally the distal one divides first (*figs. 11, 12*). These vertical walls are then followed by others at right angles to them in each cell so that the young organ consists of two or three tiers of four cells each. In each cell of each tier now appears a periclinal wall separating it into an inner spermatogenous cell and a peripheral wall-cell. This periclinal division begins at the base of the antheridium and progresses toward the apex (*figs. 19–23*), so that the interior spermatogenous cells are finally completely enclosed by the enveloping wall. Further divisions in the latter are entirely radial, so that it remains a single layer of cells in thickness.

The young antheridium now increases rapidly in size. The stalk divides transversely and vertically so that it ultimately consists of 5 or 6 tiers of about four cells each (*figs. 26–29*). The cells of the interior divide transversely (*figs. 24, 25*) and vertically (*figs. 26–29*), so that groups of cuboidal cells result. The original division-walls remain evident even in the mature structure. *Figure 29* represents an antheridium about one fourth to one third grown. The mature organ is similar in form but is much larger and contains a much greater number of cuboidal cells, formed by repeated division of the inner cells. A group of such cells from a fully grown antheridium is shown in *figure 30*. The next division in each cuboidal cell is diagonal, so that two triangular cells or spermatids result (*fig. 31*). According to Ikeno ('03) and Campbell ('05), this final diagonal division is unaccompanied by a wall in *Marchantia* and *Fimbriaria*. My own preparations stained with Delafield's hematoxylin, which brings out cell-walls clearly, shows

diagonal walls very distinctly in some of the cells, but not in all, so that they seem to disappear soon after being formed. The nuclear phenomena accompanying the production of the spermatids and their transformation into spermatozoids, together with the changes in the blepharoplast and the development of the cilia have not been specially studied, since they have been so recently worked out by Ikeno ('03).

The writer has not yet observed the explosive discharge of the spermatozoids, which is so easily seen in *Conocephalum* when the moisture conditions are right. The same phenomenon probably occurs also in *Marchantia*, and one can easily see how it might be useful in effecting fertilization in those archegonia which are matured after the elongation of the stalk of the gametophore.

ARCHEGONIUM

In the vicinity of Ithaca, the young archegoniophores begin to appear early in May. Archegonia mature and fertilization usually takes place by the time the stalk begins to elongate. The necks of such mature organs are strongly curved outward toward the margin of the receptacle. If the first-formed archegonia are fertilized, few are produced subsequently, but if fertilization is not effected they continue to develop in numbers even after the stalk is somewhat elongated. The necks of the later-formed organs are nearly straight. *Figures 32* to *69* were made from material collected when the stalks of the archegoniophores had just begun to elongate, and when mature antheridia were present on adjacent plants. It was gathered May 9, 1907, and fixed in Gilson's solution. The sections are 8–10 μ thick and stained in Delafield's hematoxylin.

The archegonia arise in radiating rows from the tissue between the lobes on the underside of the gametophore. The youngest are nearest the stalk and the oldest near the margin. The development accords in general with that usual in the Marchantiales, but since it differs in some particulars it seems best to give a brief account of the whole process. A superficial cell pushes outward beyond its fellows and its distal part is cut off by a transverse wall. The hemispherical cell thus formed is the mother-cell of the archegonium (*figs. 32, 33, 40*), and may be recognized by its deeply

staining contents. I cannot confirm the statement of Strasburger ('69) that this mother-cell is divided into two by a transverse wall, but the first division-wall is obliquely vertical and curved, and divides the mother-cell into two unequal cells (*figs. 34, 35, 63*). The second wall is in the larger cell, and is likewise obliquely vertical and curved (*figs. 36, 37*), cutting both the first division-wall and the wall of the mother-cell (*fig. 38*). A third similar wall cuts both the first and second (*cf. fig. 46*). The young archegonium has thus been segmented into an axial cell, triangular in transection, bounded by three peripheral ones. The axial cell is next divided by a transverse wall into a distal cover-cell and a proximal mother-cell of the axial row (*figs. 39, 40*). The cover-cell may segment at once (*fig. 41*), but more often it remains entire for some time (*cf. figs. 42–65*). Ultimately it becomes divided into four by two walls at right angles to each other (*figs. 47, 67, 57, et seq.*). Each of the three peripheral cells next divides by a transverse wall near the middle (*figs. 42, 43*), and these are soon followed by a corresponding one in the axial cell dividing it into a proximal central cell and a distal neck-canal mother-cell (*figs. 44, 45*). These last divisions have separated the young archegonium into two regions: the neck and the venter. About the same time each of the three peripheral wall-cells divides radially so that the wall consists of six rows of cells (*fig. 46*). Although the wall of the venter undergoes further radial division (*fig. 59*), six remains the constant number in the neck (*figs. 60, 66*).

Meanwhile the cell or cells immediately beneath the archegonium, from which the mother-cell was originally derived, grow outward (*figs. 37, 39, 40*), and divide transversely, forming what at first appears to be a stalk of the archegonium (*figs. 43–45*), but what really becomes the proximal cells of the wall of the venter (*cf. figs. 48–65*). In the young archegonium shown in *figure 34* this has taken place unusually early. It will thus be seen that the archegonium is not entirely derived from the original hemispherical mother-cell.

The young archegonium now undergoes a period of growth. The axial cells elongate, the central cell becoming the larger with a conspicuous nucleus. The wall-cells undergo repeated trans-

verse division, and those of the venter radial division also (*figs. 48–54*). The neck-canal mother-cell now divides transversely into two (*figs. 55, 56*), and then each of these into two, making four neck-canal-cells (*fig. 58*). The central cell then divides unequally into a distal ventral canal-cell and the larger egg. The writer does not think that a definite cell-wall is laid down in this last division. If it is, it disappears very soon, for the two cells are separated by a space in almost every instance (*fig. 61*). As a rule the central cell does not divide until after the four neck-canal-cells have been formed, but quite a number of instances were noted in which it had segmented when only two canal-cells were present (*fig. 57*).

All the parts of the archegonium having been differentiated, further development is in the nature of expansion or enlargement of the parts already formed. Up to this time the organ has been nearly cylindrical, but after the division of the central cell the venter becomes somewhat swollen or thickened owing to the enlargement of the egg within (*figs. 62–65, 68, 69*). The cytoplasm stains very intensely and the nucleus is large and conspicuous. The neck elongates by repeated transverse division of the wall-cells, and sometimes becomes very long and curved. The neck-canal-cells elongate and the separating walls soon disappear (*figs. 65, 68*). While four is the usual number of cells, their nuclei occasionally divide so that six or seven sometimes appear (*figs. 65, 68*). In one case (*fig. 68*) the cytoplasm of one of the cells had segmented so that five distinct masses were present. As the archegonium approaches maturity, the ventral canal-cell and the neck-canal-cells become disorganized and coalesce into a slender mucilaginous strand in the cavity of the neck. Soon the cover-cells break apart and the mass exudes, leaving an open channel to the egg (*fig. 69*). The latter becomes nearly spherical and stains very deeply. No indication of a "receptive spot" was observed.

EMBRYO AND SPOROGONIUM

The sporogonia of *Marchantia* develop rapidly. Archegonia are ready for fertilization in May and fully mature sporogonia may be found in the latter part of June or in July. Part of the material collected for archegonia May 9, 1907, was kept in the laboratory

under a bell-jar for five days, when it was fixed in chrome-acetic solution. *Figures 70–90* were made from this collection. *Figures 91–101* are from plants killed in Flemming's solution June 9, 1900. The sections are 8–10–12 μ thick and stained in Delafield's hematoxylin.

The unfertilized egg of *Marchantia* is nearly spherical in form, and is stained intensely by Delafield's hematoxylin. After fertilization it elongates slightly, becomes surrounded by a wall, and is stained with difficulty and diffusely with the same reagent (*figs. 70, 71*). This difference in staining capacity is marked and continues until the embryo has become many-celled (*fig. 93*). Another conspicuous reaction to stain is shown by the inner surface of the wall of the archegonium, which becomes deeply colored, so that in sections the pale embryo stands out in bold relief against the dark background (*figs. 70, 76, 81, 82, et al.*) The first division-wall in the fertilized egg is obliquely transverse. *Figures 72–76* show longitudinal sections of five embryos at this stage. These and the subsequent figures have been arranged so that the axes of the archegonia are parallel. In *figure 75* the wall is transverse, while extremes of obliquity are shown in more advanced embryos in *figures 77* and *84*. The second wall is perpendicular to the first, dividing the embryo into quadrants (*figs. 77–81*). The third (*fig. 82*), at right angles to the first and second, divides it into octants.

The next divisions are anticlinal (*figs. 83–90*), and are placed at such a peculiar angle with the second and third walls that essentially similar patterns are presented in both longitudinal and transverse sections. This is made evident by comparing *figures 80–88* with *89* and *90*. As a rule anticlinal division has not proceeded far before periclinal walls begin to be laid down (*figs. 83, 85–87*). Further divisions are anticlinal, periclinal, and radial, without definite sequence, until a subspherical ball of cells is produced (*figs. 91–93*), in which the primary division-walls may usually be clearly recognized. Up to this time the embryo has increased but little in size, so that its component cells become successively smaller as division progresses (*cf. figs. 70–93*).

While the above-mentioned development is proceeding in the embryo, other and more conspicuous changes are taking place in the venter of the archegonium and in the tissue at its base. In

the first place the collar at the base of the archegonium, which is inconspicuous before fertilization (*figs. 63, 69*), by transverse division of its cells grows rapidly outward until it forms a tubular sheath, the pseudoperianth, surrounding the venter, and ultimately projecting far beyond it. This is always a single layer in thickness (*figs. 70, 76, 88, 92, 94*). In the second place, periclinal division begins in the wall of the venter, and continues until two or three layers of cells are formed at the sides of and above the embryo. The tissue thus formed is the calyptra, which serves as a protective covering for the growing embryo (*figs. 70, 71, 76, 81, 82, 88–90, 92, 94–98*). The contents of its cells soon become richer so that it is stained more deeply.

The third series of changes is in the base of the venter and in the cells immediately beneath it, from which the pseudoperianth arises (*fig. 70*). Division takes place in all directions so that the base, originally narrow and rarely more than three cells across, becomes broad and massive (*figs. 70, 76, 88, 92, 94*). The cells thus formed from the base of the archegonium are generally smaller than those of the adjacent gametophore (*fig. 94*), and soon become rich in protoplasmic content and stain deeply.

The embryo and surrounding tissues now enlarge rapidly and the contents of all the cells increase in staining capacity (*fig. 94*). This is especially noticeable in the tissue beneath the embryo, derived from the base of the archegonium. The embryo itself becomes nearly spherical (*figs. 94–97*), and then broader than long (*figs. 98, 99*). The first indication of its differentiation into parts is a change in the staining capacity of the cells. Those in the distal half become richer in protoplasmic content, and form the capsule, while those of the proximal half stain with less avidity, and give rise to the stalk and foot (*figs. 95, 96*). An inspection of the embryo shown in *figure 95* shows that the stalk and capsular halves are separated by the first transverse division-wall, and this is usually the case. That it is not always true, however, is shown in *figure 96*. In this embryo the original walls were decidedly oblique, as in *figures 77* and *84*. In such cases the first division-wall does not separate the embryo into the stalk and capsular halves, but this differentiation is determined by other influences. In general it is true that, whatever be the direction of the

first division-wall, the proximal cells constituting about one half of the embryo give rise to the stalk and foot, while those of the distal half become the capsule. The line of demarcation between them is not always clear-cut, and generally coincides very nearly with the first transverse wall; but often it does not so coincide, and certainly does not necessarily do so.

As the young sporogonium enlarges, the superficial cells of the capsular portion stain less deeply and become sharply set off as an outer sterile wall of a single layer of cells enclosing the deeply staining sporogenous tissue within (*fig.* 97). The cells of the latter at this time are irregularly isodiametric, and similar to those of the stalk half. In the sporogonium figured one can detect a slight bulging of the proximal tissue of the stalk to form the beginning of the foot.

A more advanced and very interesting stage is shown in *figure* 98. The whole structure has become broader; the wall is sharply differentiated from the sporogenous tissue within; the cells of the latter have increased in number, and most of them have elongated somewhat in a direction parallel to the axis of the archegonium; the proximal cells of the stalk have become richer in contents, and are closely applied to the tissue at the base of the archegonium, into which they have begun to penetrate to form the foot. It should be noted that the cells of the archegonium adjacent to the foot are not crushed out nor flattened, but are plump and the contents stain deeply.

A still more advanced condition is shown in *figure* 99. The foot has penetrated more deeply into the basal cells of the archegonium, and has expanded laterally, forming a "pileus-shaped" absorbent organ, the cells of which are filled with deeply staining food material in the form of elliptical bodies. The capsular portion is broad, the sporogenous cells numerous and plainly elongated. In neither of the sporogonia shown in *figures* 98 and 99 is the line of demarcation between the stalk and sporogenous tissue regular, so that it probably does not exactly conform to the original transverse wall of the embryo.

In the still older sporogonium shown in *figure* 100, the foot has become more massive and has penetrated more deeply into the tissue of the base of the archegonium. The cells of the sporog-

enous tissue have separated completely from one another, and have elongated. The great majority are narrowly triangular in outline, and are frequently arranged in pairs end to end. A few, however, are narrow and slender, and present the first indications of a differentiation between sporogenous cells and elaters. In the much larger embryo shown in *figure 101*, the distinction between fertile cells and elaters is more marked. The former have lost to some extent the regular triangular outline, while the latter are much more slender and sometimes flexuous. The two kinds of cells alternate irregularly.

In its further development the sporogonium elongates rapidly until it becomes oblong or elliptical in general outline. The stalk, however, remains for a long time very slight. At the same time the separate cells filling the capsule increase in size. The elaters become long and fusiform, and the contents arranged in a spiral manner next the wall. While the sporogenous cells increase in size they do not seem to increase in number after the separation shown in *figure 100*. They soon divide, however, by transverse, or by transverse and longitudinal walls into groups of eight, rarely four, cells (*fig. 102 a–h*), which do not separate but remain connected together. These are the spore-mother-cells. If the division is transverse only, the mother-cells are arranged in rows (*fig. 102 a, d, e*). If longitudinal division also occurs, the mother-cells are biseriate or subbiseriate in the group (*b, c, f, g, h*). A very characteristic condition is shown in figures *c* and *h*, in which the original cells were subtriangular in outline and arranged in pairs, as appears so often in *figures 100* and *101*. The resulting groups of mother-cells are also subtriangular in form and still remain in pairs. The mother-cells are irregular in shape, and are flattened where contiguous ones come in contact.

The mother-cells now increase in size as the capsule expands. The details of their division have not yet been worked out, but each gives rise to four tetrahedral spores (*fig. 103 i–m*). The spores remain connected in the tetrads for a long time, and the latter, as well, cling together nearly as long in their original groups. The tetrads, however, seem to become free from one another before the spores separate (*fig. 103 m*).

About the time of the division of the spore-mother-cells, ac-

tivity begins in the stalk. Each component cell divides repeatedly in a direction transverse to the long axis of the sporogonium, so that very regular rows of cells are produced between the foot and the capsule. The latter is thus pushed outward until the calyptra is ruptured at its apex. At first the cells of the stalk are broader than long, but later they increase greatly in length so that the stalk elongates, pushing the capsule beyond the surrounding perianth. As the capsule dries it ruptures at the apex into numerous lobes so that the spores and elaters are set free.

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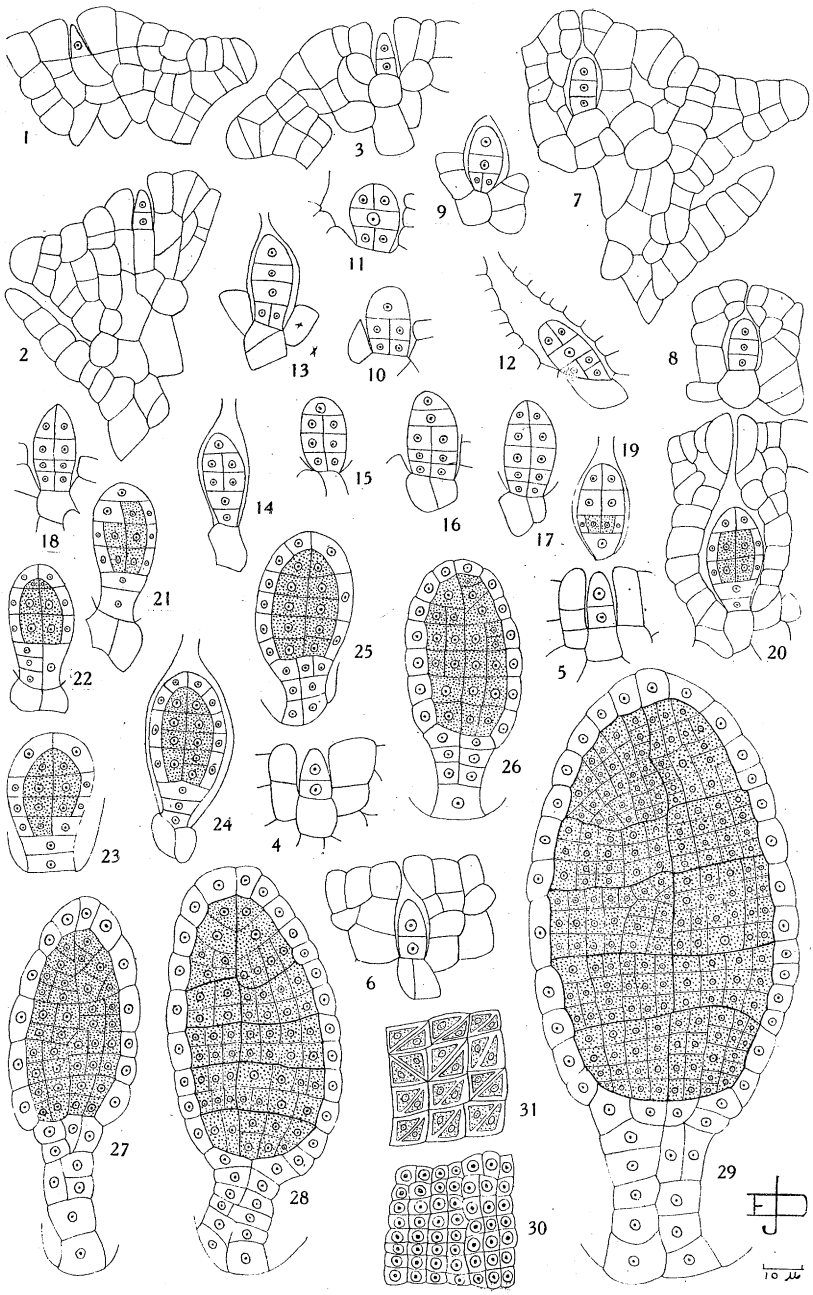

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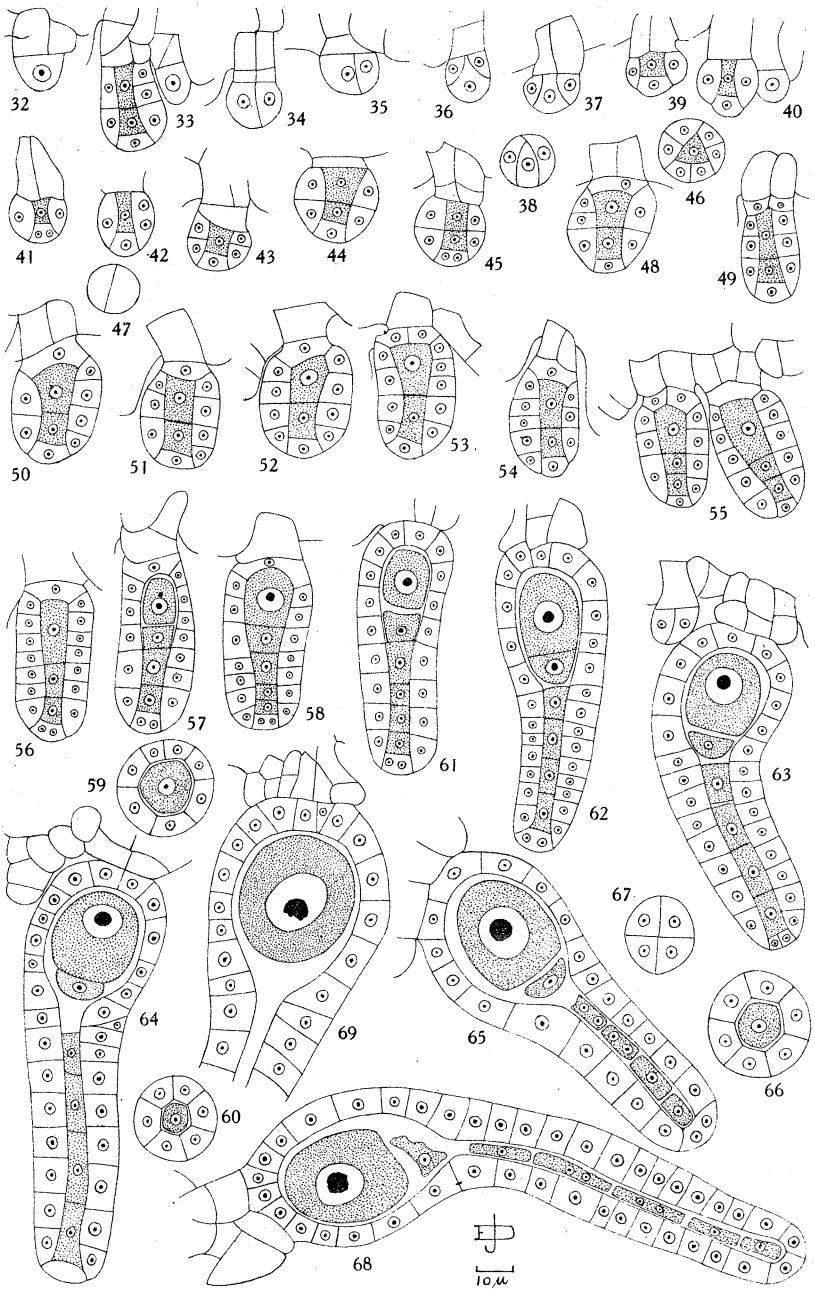

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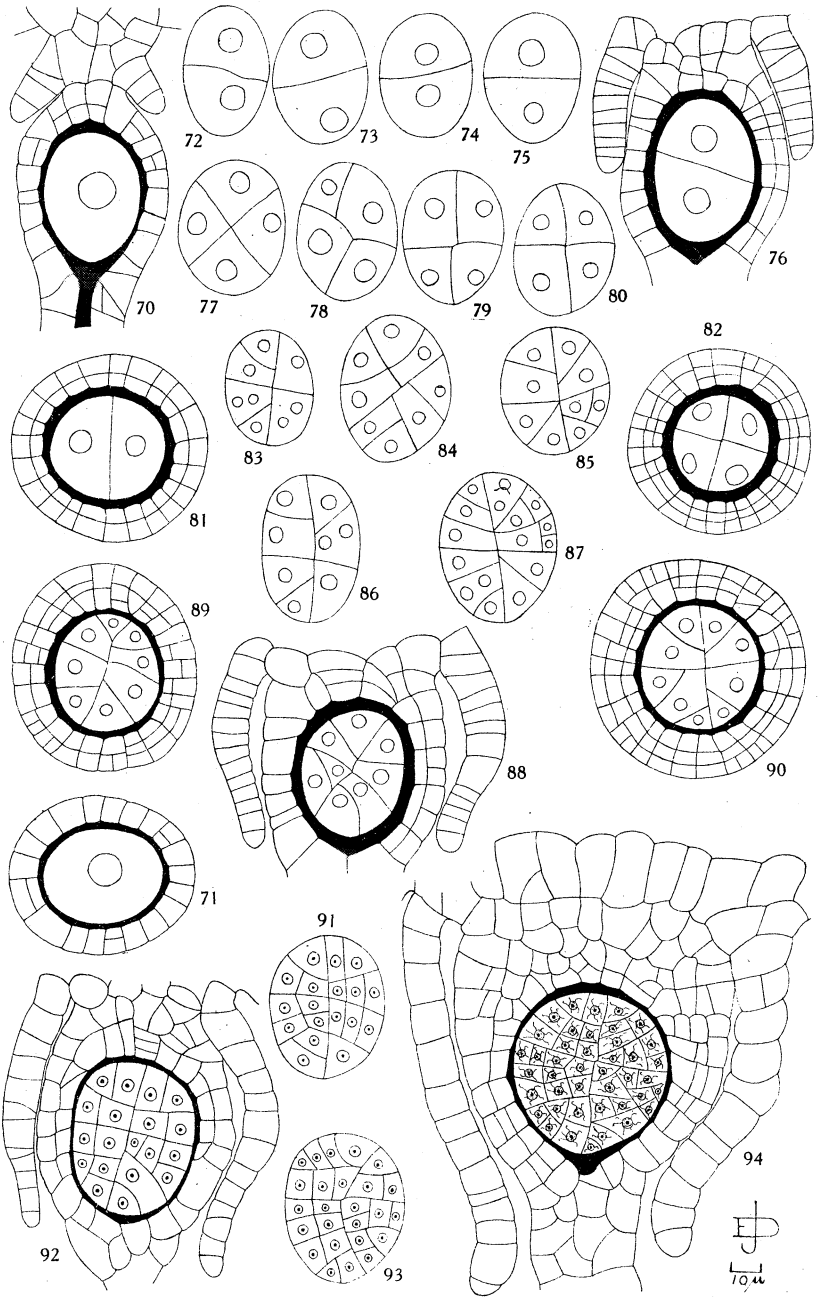

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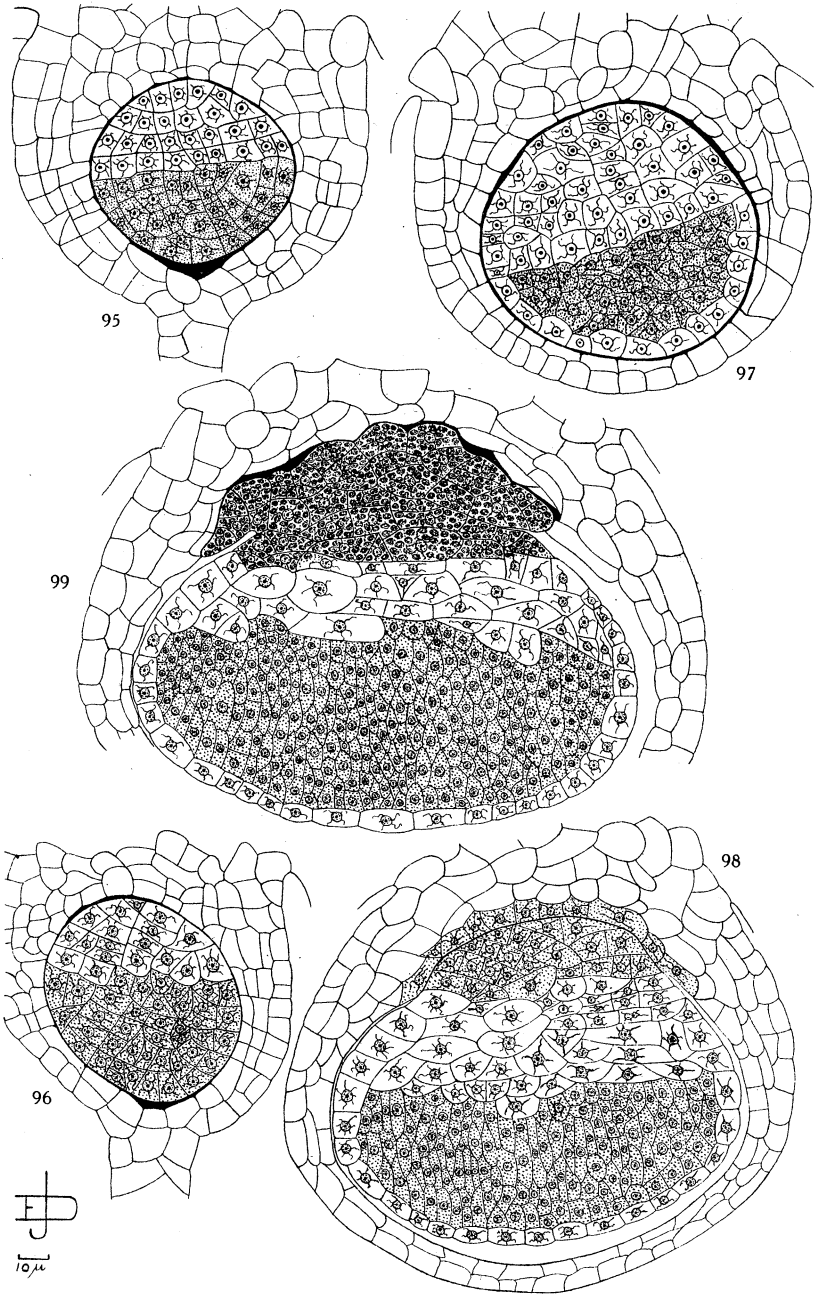

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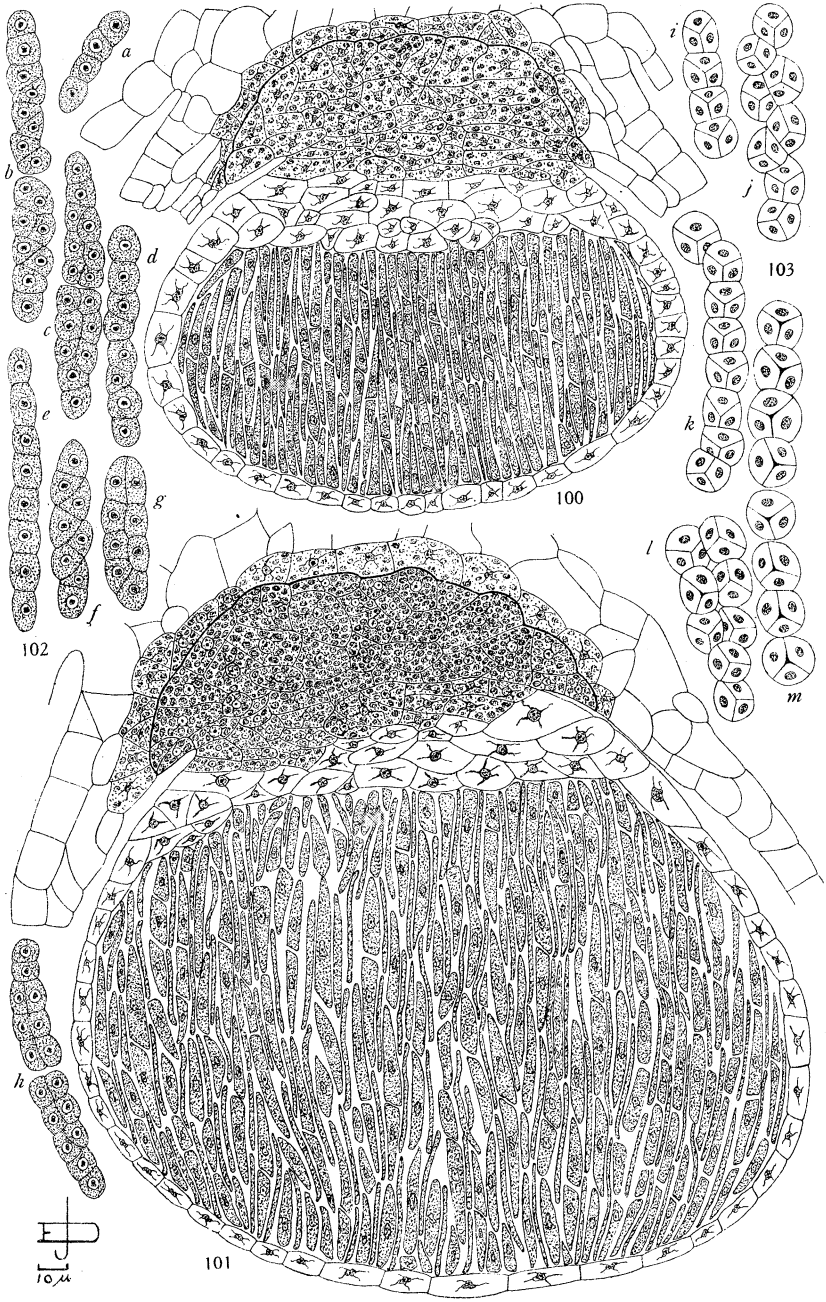

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Explanation of figures (plates 21-25)

All figures were drawn with the aid of the camera lucida. Figures 1–30, 32–69, 102, and 103, were drawn with the B. & L. one-eighth objective and one-inch ocular. Figure 31 was drawn with the one-twelfth objective and one-inch ocular. Figures 70–101 were drawn with the one-sixth objective and one-inch ocular. The exact magnification is indicated with each plate.

ANTHERIDIUM

FIG. 1. Longitudinal section of gametophore showing 1-celled rudiment of the antheridium.

FIGS. 2, 3. The antheridial rudiment has divided by a transverse wall into the mother-cell of the stalk and mother-cell of the antheridium proper.

FIGS. 4, 5. Same as last but from transverse section of the gametophore; antheridium enlarging.

FIG. 6. Same as last but young antheridium becoming more deeply buried by the upgrowth of the surrounding cells.

FIGS. 7, 8. The whole organ more deeply buried; antheridial mother-cell divided by a transverse wall.

FIG. 9. As in last but division beginning in mother-cell of the stalk.

FIGS. 10–12. As in last but vertical division beginning in mother-cell of antheridium proper.

FIG. 13. Antheridial mother-cell divided by two transverse walls.

FIGS. 14–18. As in last but showing variations in division in the stalk, and successive steps in vertical division of antheridium.

FIGS. 19–23. Steps in the periclinal division of the antheridium to separate the wall from the spermatogenous tissue within.

FIGS. 24, 25. Antheridium enlarging; beginning radial division in the wall, and transverse division of spermatogenous tissue.

FIGS. 26–28. Further radial division in the wall; successive steps in division of spermatogenous tissue by transverse and vertical walls into cuboidal cells; increasing massiveness of the stalk.

FIG. 29. Antheridium one fourth to one third grown; original vertical and transverse walls plainly evident.

FIG. 30. A block of cuboidal cells from a mature antheridium just before their diagonal division to form the spermatids.

FIG. 31. A block of cuboidal cells from same antheridium as figure 30, showing diagonal division to form the spermatids. Note that in some of the cells diagonal walls appear between the spermatids. One-twelfth objective.

ARCHEGONIUM

FIGS. 32, 33, 40. Mother-cell of the archegonium cut off from the cell of the gametophore from which it has arisen.

FIGS. 34, 35. The mother-cell divided by one obliquely vertical wall.

FIGS. 36, 37. The mother-cell divided by two obliquely vertical walls.

FIG. 38. Transection of young archegonium, showing relation of the two walls.

FIGS. 39, 40. The axial cell divided by a transverse wall to form the cover- and the mother-cell of the axial row.

FIG. 41. Cover-cell divided.

FIG. 42. One peripheral cell divided transversely.

FIG. 43. All peripherals divided transversely.

FIGS. 44, 45. Peripherals and mother-cell of axial row divided transversely, the latter into the central cell and mother-cell of the neck-canal-cells. The young archegonium is now differentiated into the neck and venter.

FIG. 46. Transection of venter at this stage.

FIG. 47. Transection of cover of same archegonium as in figure 46.

FIGS. 48–54. Steps in the radial division of the wall and increase in length of the archegonium.

FIGS. 55, 56. The neck-canal mother-cell has divided transversely into two.

FIG. 57. An abnormal condition in which the ventral canal-cell has been cut off before the formation of four neck-canal-cells.

FIG. 58. Four neck-canal-cells, central cell undivided.

FIG. 59. Transection of venter of about the stage of figure 58.

FIG. 60. Transection of neck of same archegonium.

FIG. 61. Central cell divided into the egg and ventral canal-cell.

FIGS. 62–64. Archegonium enlarging; four neck-canal-cells.

FIG. 65. Nuclei of two of the neck-canal-cells divided.

FIG. 66. Transection of neck of about the stage of figure 65.

FIG. 67. Transection of cover-cells of same archegonium as in figure 66.

FIG. 68. Archegonium mature; canal-cells ready to disintegrate; five neck-canal-cells with seven nuclei.

FIG. 69. Base of archegonium, egg ready for fertilization.

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FIG. 70. Base of an archegonium containing a fertilized but undivided egg. Note the beginning pseudoperianth.

FIG. 71. Transection of similar stage.

FIGS. 72–76. Fertilized egg once divided. In 76 note the growth of the pseudoperianth and increasing tissue at base of archegonium.

FIGS. 77–80. Embryo divided into quadrants.

FIG. 81. Transection of quadrant stage.

FIG. 82. Transection of octant stage. In 81 and 82 note the periclinal division in the wall of the venter.

FIGS. 83–88. Steps showing formation of anticlinal walls in each octant. Figures 83, 85–87, show also the beginning of periclinal walls. In 88 note the increasing pseudoperianth and tissue at base of the archegonium.

FIGS. 89, 90. Transections of similar stages.

FIGS. 91–93. Older embryos. Note the slight increase in size over 70.

FIG. 94. Embryo increasing in size. Note the massive base of the archegonium and the pseudoperianth.

FIG. 95. An older stage. Note that the distal half stains more deeply, the two halves being separated by the original transverse wall.

FIG. 96. Similar to last but the distal deeply staining portion is not separated from the proximal paler part by the original transverse wall.

FIG. 97. An older larger stage in which the distal half of the embryo is differentiated into an outer wall of one layer of cells enclosing the deeply staining sporogenous tissue within, and the basal portion of the proximal half has begun to grow toward the tissue at the base of the archegonium to form the foot.

FIG. 98. The deeply staining foot has begun to penetrate the base of the archegonium, and the cells of the sporogenous tissue have begun to elongate somewhat.

FIG. 99. Sporogenous cells about as in figure 98, but the foot has pressed into the base of the archegonium and expanded to form a pileus-shaped absorbent organ, which is filled with food material.

FIG. 100. A more advanced stage in which the sporogenous cells have separated from one another and become long-triangular in shape and often arranged in pairs.

FIG. 101. Somewhat older than the last. The sporogenous cells have become differentiated into two kinds: stout ones and more slender elaters.

FIG. 102. The stout cells of the last figure have become divided into 8 (rarely 4) spore-mother-cells, those of each group being arranged either in single rows (*a*, *d*, *e*) or in a triangular or subbiseriate manner (*b*, *c*, *f*, *g*, *h*). The groups are frequently arranged in pairs (*b*, *c*, *h*) corresponding to the paired cells of figures 100 and 101.

FIG. 103. An older stage in which each spore-mother-cell has divided into four spores, the tetrads still clinging together in groups of 4 or 8. In *m*, the oldest stage, they have begun to separate but still form an easily recognized group.